

UC San Diego

UC San Diego Previously Published Works

Title

Advection and zooplankton fitness

Permalink

<https://escholarship.org/uc/item/7069c41k>

Journal

Sarsia, 83(2)

ISSN

0036-4827

Authors

Eiane, Ketil
Aksnes, Dag L
Ohman, Mark D

Publication Date

1998-06-02

DOI

10.1080/00364827.1998.10413674

Peer reviewed

ADVECTION AND ZOOPLANKTON FITNESS

KETIL EIANE, DAG L. AKSNES & MARK D. OHMAN

SARSIA

EIANE, KETIL, DAG L. AKSNES & MARK D. OHMAN 1998 06 02. Advection and zooplankton fitness. – *Sarsia* 83:87-93. Bergen. ISSN 0036-4827.



Successful adaptation to the environment by zooplankton is constrained by the agents of mortality (starvation, predation) and losses due to advection. A fitness measure which explicitly includes risk of advective loss is presented. The authors show that as horizontal current speeds and vertical shear increase, the behavioral strategies that maximize fitness of zooplankton possessing different life history strategies are affected. For a *Calanus finmarchicus*-type life history, fitness is maximized by diel vertical migrations when advection risk in surface waters is low and by spending less time in the surface layers as flow rate increases. For a *Paracalanus parvus*-type life history, vertical migration is postulated to occur as advective loss increases. The geographic length scale of the habitat of residence also affects the optimal mode of habitat selection. In the *Calanus* case an abrupt change in the optimal vertical migration pattern is postulated as a function of length scale of habitat and rate of advection.

Ketil Eiane (corresponding author, e-mail: ketil.eiane@ifm.uib.no) & Dag L. Aksnes, University of Bergen, Department of Fisheries and Marine Biology, Bergen High-Technology Centre, N-5020 Bergen, Norway. – Mark D. Ohman, Marine Life Research Group 0227, Scripps Institution of Oceanography, La Jolla, CA 92093-0227, USA.

KEYWORDS: Fitness; zooplankton; advection.

INTRODUCTION

HOUSTON & al. (1993) pointed out that when animals can choose from a range of feeding options, often those options with a higher energetic gain carry a higher risk of predation. This seems to be particularly true for the herbivorous zooplankton. The bulk of their potential food is produced in a narrow layer close to the surface which they have to approach in order to meet their energetic demands. Their predators, however, are adapted to the obvious need for their prey to concentrate in this layer and thereby turn the energy-rich productive layer into a risky habitat for the herbivores. Deeper in the water column darkness reduces the effectiveness of visually searching predators (LAMPERT 1989; AKSNES & UTNE 1997), and offers space for dilution making non-visual predators less effective (OHMAN & al. 1983; EIANE & al. 1997). Thus, the deeper habitat is generally much safer, but represents an energetic disaster in the long run. For the herbivore, there are basically two ways of adapting to this situation (McLAREN 1963; AKSNES & GISKE 1990; HOUSTON & al. 1993). The first is to stay in the productive layer by utilizing the energy surplus in a way that produces offspring at a higher rate than (or equal to) the predation rate. The second is to make

excursions to the deep habitat, preferably at times when predation risk in the productive layer is at the highest, in order to increase survival.

It is widely recognized that the principal benefit of downward migration is to reduce the risk of predation (STICH & LAMPERT 1981; LAMPERT 1989; OHMAN 1990). However, some authors have also addressed the effect of advection combined with vertical migratory behavior on the distribution (dispersal or retention) of planktonic organisms (HARDY & GUNTHER 1935; HARDY 1936, 1938; FRASETTO & al. 1962; BOSCH & ROWLAND TAYLOR 1973; WRUBLEWSKI 1982). Retention in a population's habitat (i.e. avoiding transport losses) is crucial for contributing to the next generation (ILES & SINCLAIR 1982; SINCLAIR 1988). Optimality theory in ecology sometimes gives the impression that individuals are able to trade-off several opposing forces to make optimal decisions, resulting in the highest possible fitness. In this view, it may seem irrelevant whether a copepod is transported out of a given habitat, as long as it remains alive and reproductive. However, organisms are not 'fitness maximizers', but 'adaptation executioners' (WRIGHT 1994): A population's gene pool will consist of the contributions from those individuals that reproduced within the spatial boundaries of the

population. Thus any strategy resulting in its bearers reproducing after they have been transported out of the populations spatial range, will not contribute to the gene pool of the population they left. Rather, a strategy that makes an individual stay – even at some reproductive cost – may spread in the gene pool. Thus, for a zooplankton population to persist within a certain habitat, adaptation both to the risk of being killed and to the risk of being transported out of the habitat is essential. In the present study we combine advective influence and predation risk into a common fitness measure in order to evaluate the adaptive significance of vertical migratory behavior. Assuming one predatory regime, but different advective regimes, we make a quantitative analysis showing that vertical migration behavior should, under certain circumstances, represent a behavioral adaptation to the risk of being lost from a habitat.

METHODS

Optimal behavior

We provide a general analysis of how advection may influence zooplankton behavior by applying static optimization. We will base our fitness measure on the realized instantaneous rate of increase (r), assuming that the populations can choose between two habitats (h_1 and h_2), and that each of these habitats offer different possibilities in terms of fecundity (m), probability of survival (l), generation time (T) and advective rates (v). As HOUSTON & al. (1993) we will use a variable u that characterizes the animal's behavior, where $0 \leq u \leq 1$. A value of 1 corresponds to the case where the individual spends all its time in h_1 (which denotes our surface habitat), while $u = 0$ corresponds to the case where all the time is spent in h_2 (deep habitat). Hence, the

fecundity, probability of survival, generation time, advective rates, and thereby the fitness of a strategy (ρ) will depend on the actual time allocation between the two habitats (i.e. the value of u):

$$1 = \int_{T(u)}^{\infty} l_x(u) m_x(u) e^{-\rho(u)x} dx \quad (1)$$

(see Table 1 for explanation of symbols). The optimal behavior (u^*) is found by maximizing ρ . For analytical tractability we will assume time-invariant $l_x(u)$, $m_x(u)$, $T(u)$, and $\rho(u)$ functions (see below).

Predation and advection

We will consider a zooplankton population to be confined to a certain part of the ocean (H) in the sense that if individuals are lost (due to advection) from this geographical area, further contributions to the local gene pool are not possible (i.e. the population is isolated in the sense that immigration to H does not occur). The two habitats h_1 and h_2 are vertical subhabitats of H . The horizontal extension of H will be characterized with a length scale, L (m), and the advective loss rate from H is different for h_1 and h_2 and is denoted v_{h_1} and v_{h_2} (m s^{-1}), respectively (Fig. 1). Thus the rate of advective loss is a function of behavior:

$$a(u) = v(u)L^{-1} \quad (2)$$

Specifically, we will assume that the horizontal velocity of the surface habitat (v_{h_1}) is greater than that of the deep habitat (v_{h_2}). Thus individuals spending time in h_1 are lost more rapidly from H than if the same time is spent in h_2 . We will consider the case where v_{h_1} and v_{h_2} are characterized by different speeds only, as well as the case where the two have opposite directions.

Table 1. Symbol explanations.

		Unit
$a(u)$	Advective loss rate	s^{-1}
$d(u)$	Predation rate as a function of u	s^{-1}
h_1	Surface habitat	-
h_2	Deep habitat	-
l_x	Expected survival to time x	-
\bar{L}	The length scale of the habitats	m
m	Fecundity	ind. ind. ⁻¹
M	Predation risk	-
$T(u)$	Generation time as a function of u	s
u	Proportion of time allocated in h_1 (relative to $(u-1)$ in h_2)	-
$v(u)$	Transport rate out of the habitats as a function of u	m s^{-1}
$\rho(u)$	Advection-corrected per capita rate of increase as a function of u	s^{-1}

The daytime and nighttime predation risks of the surface habitat are defined M_{hd} and M_{hn} respectively. The deep habitat is characterized by a single risk M_{h2} . We will assume that the daytime risk of the surface habitat is higher than the nighttime risk, and that the surface nighttime risk is higher than the risk of the deep habitat ($M_{hd} > M_{hn} > M_{h2}$). In our simulations night and day are both 12 h periods. Hence, an animal spending all its time in the surface layer will face a realized predation rate equal to the average of the daytime and nighttime risks, $d(u=1) = 0.5(M_{hd} + M_{hn})$. For an animal switching between the two habitats we will assume that the deep habitat is occupied only during daytime in order to minimize the all-over predation risk (as long as $u > 0.5$). If u drops below 0.5, however, nighttime also has to be spent in the deep habitat, and no time has to be spent in the surface layer at daytime. Mathematically this is expressed:

$$d(u) = (u-0.5)M_{hd} + 0.5M_{hn} + (1-u)M_{h2} \quad \text{for } u > 0.5$$

$$d(u) = uM_{hn} + (1-u)M_{h2} \quad \text{for } u \leq 0.5 \quad (3)$$

Thus we can describe total loss (predation and advection) from H as functions of behavior and define the survival probability to any given time x by:

$$l_x(u) = e^{-(d(u)+v(u)L)x} \quad (4)$$

Generation time and fecundity

We will assume that the generation time equals T_{h1} if all time is spent in the surface habitat (h_1). The generation time increases as more time is spent in the deep habitat according to:

$$T(u) = T_{h1}/u \quad (5)$$

Thus the generation time doubles if the time is divided equally between the two habitats ($u = 0.5$), and that generation time approaches infinity as u approaches 0 (i.e. all time spent in the deep habitat). This is in accordance with the empirical relations for adult *C. finmarchicus* dividing its residence between two habitats differing by 9.5 °C (CORKETT & al. 1986).

Although body size and fecundity are often correlated with generation time, we will assume that fecundity is independent of u :

$$m(u) = m(h_1) = m(h_2) \quad (6)$$

Note, however, that birth rate is indeed influenced by u through the effect on generation time.

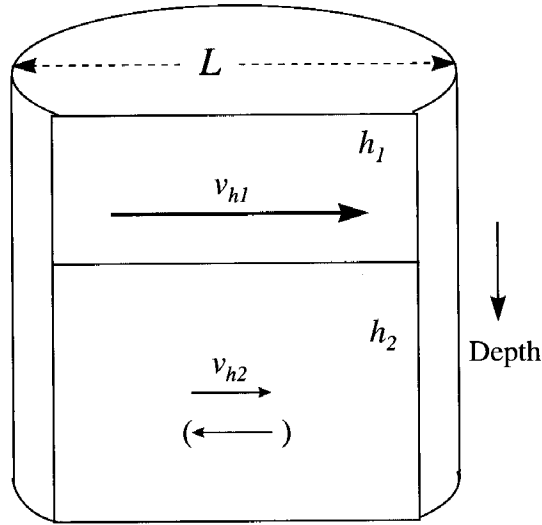


Fig. 1. The habitat (H) as described in the model. The habitat is characterized by a length scale (L), and the water column is divided into two regimes (surface subhabitat h_1 and deeper subhabitat h_2) of different advective rates (v_{h1} and v_{h2}) which may differ in strength and direction.

Inclusion of advection risk in the fitness measure

From the above equations a measure of behavior-specific expected fitness ($\rho(u)$) can be compiled as

$$1 = m \int_{T(u)}^{\infty} e^{-(d(u)+v(u)L^{-1})x} e^{-\rho(u)x} dx \quad (7)$$

which integrates to:

$$1 = \frac{m}{\rho(u) + d(u) + v(u)L^{-1}} e^{-(\rho(u)+d(u)+v(u)L^{-1})T(u)} \quad (8)$$

Eq. 8 is solvable for the fitness of a strategy (u) by iteration.

Initialization of life-history parameters

Values of generation time, fecundity and mortality risk are set according to those given by AKSNES & GISKE (1990) in their habitat profitability analyses of *Paracalanus parvus* and *Calanus finmarchicus*. These were based partly on results reported in the literature (generation time and fecundity) and mortality estimates made by AKSNES & MAGNESEN (1988). Rather than assuming two discrete habitats they assumed a continuous shift in habitat characteristics along the depth axis and this requires some modifications in the

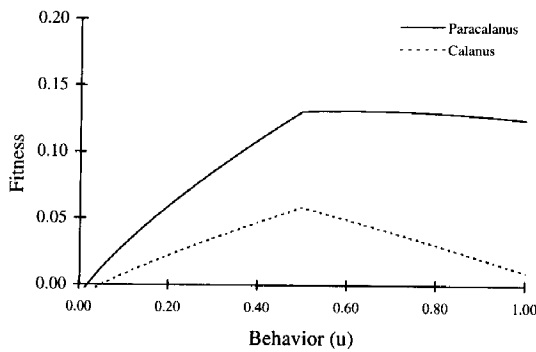


Fig. 2. Fitness (ρ) as related to behavior (u) for the *Calanus* and the *Paracalanus* cases modeled without advection.

adaptation of their parameter values: For the *Paracalanus* case we initialize Eq. 8 with a fecundity corresponding to 16 eggs d^{-1} and $T_{h1} = 12$ days which correspond to the values AKSNES & GISKE (1990) assumed for the upper five meters. For the *Calanus* case, AKSNES & GISKE (1990) varied the lifetime fecundity from 300-3000 eggs, while we will assume a fecundity corresponding to 20 eggs d^{-1} . Rather than assuming a fixed generation time as AKSNES & GISKE (1990) did in the *Calanus* case we set the T_{h1} -parameter three times higher than for the *Paracalanus* case, i.e. $T_{h1} = 36$ days. This generation time may seem short. However, T_{h1} is not the realized generation time, but a theoretical minimum time *Calanus* has to spend feeding in the surface habitat h_1 in order to mature. According to Eq. 5, if *Calanus* spends 10 % or 50 % of its lifetime in h_1 ($u = 0.1$ or $u = 0.5$), then the realized generation times become 360 and 72 days respectively. We apply the predation risks: $M_{h1d} = 0.3 d^{-1}$, $M_{h1n} = 0.1 d^{-1}$ and $M_{h2} = 0.01 d^{-1}$. These correspond to the values $0.2 d^{-1}$ and $0.01 d^{-1}$ AKSNES & GISKE (1990) calculated for the upper five meters and 70 m respectively.

RESULTS

No advection

First we re-investigate the *Calanus* and *Paracalanus* cases made by AKSNES & GISKE (1990). Their analyses were made for populations supposed not to be influenced by advection, and we therefore set the advective impact term ($v(u)L^{-1}$) of Eq. 8 equal to zero. As can be seen from Fig. 2 fitness is maximized with $0.5 \leq u < 1$ for *Paracalanus*. This means that the optimal behavior is to spend most time in the surface layer. For the *Calanus* case, however, the optimal behavior is given by u close to 0.5. In our idealized analysis, this corresponds to diel vertical migration. Hence, the result

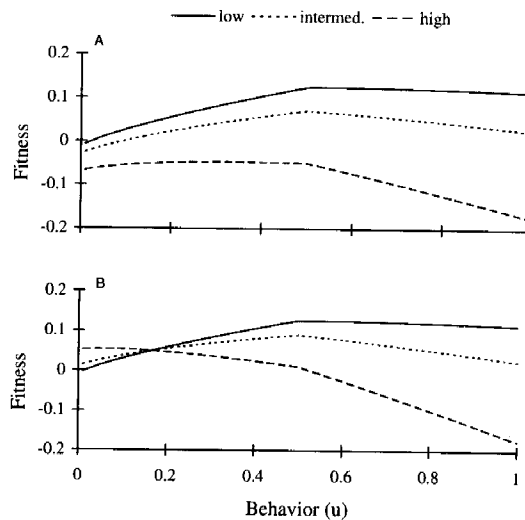


Fig. 3. Fitness (ρ) in relation to behavior for different advective regimes for the *Paracalanus* case. A. v_{h1} differs from v_{h2} in speed only. B. The two advective regimes also differ in direction.

that *Calanus* should and *Paracalanus* should not migrate is common for the present approach and that used by AKSNES & GISKE (1990).

Advection in the *Paracalanus* case

At low advective loss ($v/L = 0.01 d^{-1}$, Fig. 3A), the fitness consequence of depth selection behavior corresponds to the case without advective loss (Fig. 2), which means that most time should be spent in the surface layer. As the advective loss increases the optimal strategy shifts towards diel vertical migration. In the intermediate case ($v/L = 0.1 d^{-1}$, Fig. 3A) fitness is maximized for $u = 0.5$ although all behaviors at the range 0.5 to 1 are approximately equally fit (this means that factors not accounted for in this analysis are likely to impact optimal behavior). Although positive fitness is not achieved at the highest advective loss level ($v/L = 0.3 d^{-1}$, Fig. 3A), it is demonstrated that the behavior given by $u = 1$ now has become the least fit.

The effect of an advective regime where the direction of the current of the deep habitat is opposite, although weaker to that of the shallow habitat ($v_{h2} = -0.1 m s^{-1}$ versus $v_{h1} = 0.5 m s^{-1}$) is demonstrated in Fig. 3B. As should be expected, the adaptive significance of vertical migration is increased compared to the case where the flow direction was not considered. At the highest advective loss level ($v/L = 0.3 d^{-1}$, Fig. 3B) the optimal behavior is given by $u = 0.2$, which corresponds to the time allocation that enables the organism to maintain a

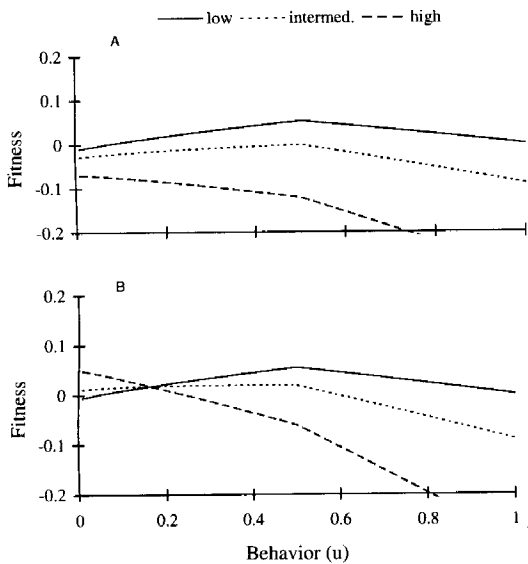


Fig. 4. Fitness in relation to behavior for different advective regimes for the *Calanus* case. A. v_{h1} differs from v_{h2} by strength only. B. The two advective regimes differ in direction.

fixed geographical position. Contrary to the non-directional case (Fig. 3A), it should now be noted that the fitness is positive for the high advective regime. At the intermediate level of flow ($v/L = 0.1 \text{ d}^{-1}$, Fig. 3B) the optimal behavior is given by diel vertical migration ($u = 0.5$).

Advection in the *Calanus* case

The fitness of the slower growing *Calanus* is more sensitive to horizontal transport than *Paracalanus* (Fig. 4A). The shift towards migrational behavior as advective impact increases is also demonstrated in the *Calanus* case. At the intermediate advective impact level ($v/L = 0.1 \text{ d}^{-1}$, Fig. 4A), the optimal behavior is still given by diel vertical migration, as in the non-advective (Fig. 2) and in the low advective ($v/L = 0.1 \text{ d}^{-1}$, Fig. 4A) case. At the highest advective impact level ($v/L = 0.3 \text{ d}^{-1}$, Fig. 4A) the fitness is highly negative (i.e. the population can not be sustained in the environment, and strategies can not adapt to it), but it is indicated that the optimal behavior is shifted towards a low u .

The effect of opposite directed currents to the fitness function is shown in Fig. 4B. Again, at low advective impact level ($v/L = 0.01 \text{ d}^{-1}$, Fig. 4B) the fitness function is unaltered compared to the case without advection (Fig. 2). At the intermediate advective impact level ($v/L = 0.1 \text{ d}^{-1}$, Fig. 4B) fitness is maximized for a rather

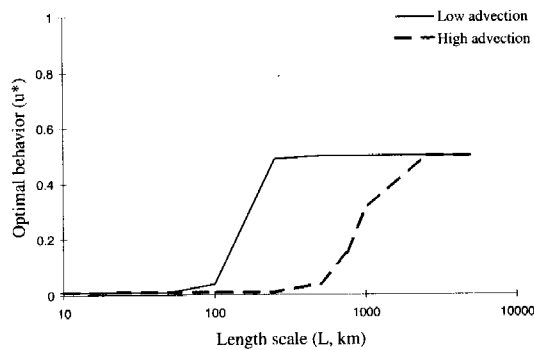


Fig. 5. Optimal behavior (u^*) for the *Calanus* case as a function of the relation between length scale (L) of the habitat and the magnitude of advection (v).

broad behavioral range ($0.2 < u < 0.5$). This is contrasted by the results for the highest advective impact level ($v/L = 0.3 \text{ d}^{-1}$, Fig. 4B). Here, the fitness function is characterized by a rather narrow positive peak. Such peaks indicate little room for individual variation in terms of migrational behavior and that highly synchronized behavior is to be expected.

Influence of habitat length scale on behavior

In previous analyses the advective impact was given by the ratio v/L . Now, we will see how changes in the absolute length scale of the habitat influences the optimal behavior being defined as the u giving the highest fitness (u^* , Fig. 5). To demonstrate this we have assumed the *Calanus* case and applied two advective regimes (low: $v_{h1} = 0.1$, $v_{h2} = -0.02$, and high: $v_{h1} = 0.5$, $v_{h2} = -0.1$). As can be seen from Fig. 5 an increase in the habitat length scale results in a shift in the optimal behavior from the high advective strategy to the low advective strategy. With the low advective rate (0.1 m s^{-1}) this shift occurs at about $L = 85 \text{ km}$, while the higher advective rate (0.5 m s^{-1}) gives a shift at a length scale that is five times higher ($L = 425 \text{ km}$). Thus, the critical length scale for shift in the optimal behavior is proportional to the strength of the flow. Although the shift in optimal behavior is abrupt as illustrated in Fig. 5, it should be noted that around the critical L , there exists a zone where a wide range of suboptimal behavioral strategies exist (see Fig. 4B, $v/L = 0.1$).

DISCUSSION

The idea that differentiated currents in different layers of the water column affect the distribution of vertically migrating zooplankton was first addressed in Hardy's

hypothesis of animal exclusion (HARDY & GUNTHER 1935; HARDY 1936, 1938). Since then vertical migration between water bodies traveling at different speeds has been suggested as a mechanism retaining planktonic organisms within habitats from which they otherwise might be exported (FRASETTO & al. 1962; BOSH & ROWLAND TAYLOR 1973; WROBLEWSKI 1982). However, the principal effect of vertical migration is believed not to reduce risk of advection, but risk of predation (STICH & LAMPERT 1981; OHMAN & al. 1983). We postulate that the risk of being advected out of the resident habitat adds to the restrictions of expected survival (l_x of Eq. 1) in that habitat much in the same way as probability of starvation and predation. Therefore strategies for vertical positioning must be tuned to fit the local advective regime for natural selection to result in adaptations to starvation and predation risks. Consider a zooplankton population residing in a well defined habitat: a semi-enclosed volume of water (e.g. a fjord), where the water column is divided in two flow regions. Above the sill depth the probability of being advected out of the system is high compared to the rather stable body of water below the sill depth (GADE & EDWARDS 1980). But, food is encountered almost exclusively in the upper region, where predation risk from visually searching predators typically is higher than at depth. Furthermore, during the productive season, temperature in the upper region tends to be significantly higher than in the deep region. In order to contribute to the gene pool of later generations of the population, vertical migration behavior (Fig. 2) will be tuned to fit the local combination of advection rates and length scale (Figs 3, 4 & 5). Otherwise the organism might be lost from the population (SINCLAIR 1988). In open waters the habitat of residence is typically less well defined, and large scale advection may distribute planktonic organisms over large areas resulting in extensive gene flow between populations (BUCKLIN & al. 1996). While biological rates (births and deaths) are believed to predominate over advective rates in the Subpolar Gyre and in the Norwegian Sea (AKSNES & BLINDHEIM 1996), advective loss due to freshwater outflow may have importance for the local production in Vestfjorden (SKRESLET & RØD 1986). Species with their primary distribution along shelf breaks (e.g. *Meganctiphanes norvegica*) face strong selective pressure against strategies failing to maintain position, since nocturnal drift into shallower areas may increase the risk of predation the following day (KAARTVEDT 1993). Others have focused on the ability of zooplankton populations or planktonic life history stages of benthic species to persist in productive habitats such as estuaries (BOSCH & ROWLAND TAYLOR 1973; CRONIN & FORWARD 1982) or in upwelling areas (WROBLEWSKI 1982), claiming

vertical migrations between layers of different speeds as the functional mechanism. Furthermore, *Acartia tranteri* migrate vertically in synchrony with the tides, and in a direction to reduce losses from a bay (KIMMERER & MCKINNON 1987).

Increased risk of advective loss tends to reduce fitness and alter the shape of the fitness function (Figs 3 & 4), thus advection affects the optimality of a strategy. Therefore strategies of habitat selection (vertical positioning) in zooplankton should be corrected for risk of advective loss. The optimal adaptation to increasing levels of this risk is to apply vertical migration (Figs 3 & 4). In habitats where the loss rate is too high or the spatial scale is too small, populations of zooplankton cannot persist (Figs 3A & 4A) and adaptation to local regimes will not take place. The zooplankton of such a habitat would therefore be expected to consist of drifting individuals, lost from other habitats, or adapted to drifting (KAARTVEDT 1993).

This analysis is kept at an extremely simplistic level. Adding realism would help explain the great variety of patterns observed in nature. However, it suffices our purpose: To show the existence of situations where horizontal transport may be a major selective factor for behavioral strategies in zooplankton.

ACKNOWLEDGMENTS

We would like to thank L. Asplin, J. Giske and G. Huse for valuable comments on an early version of the manuscript and NSF OCE-9421876 for financial support to MDO. This is a contribution from TASC (Trans Atlantic Studies of *Calanus finmarchicus*) and *Mare Cognitum*.

REFERENCES

- Aksnes, D.L. & J. Blindheim 1996. Circulation patterns in the North Atlantic and possible impact on population dynamics of *Calanus finmarchicus*. – *Ophelia* 44:7-28.
- Aksnes, D.L. & J. Giske 1990. Habitat profitability in pelagic environments. – *Marine Ecology Progress Series* 64:209-215.
- 1993. A theoretical model of aquatic visual feeding. – *Ecological Modelling* 67:233-250.
- Aksnes, D.L. & T. Magnesen 1988. A population dynamics approach to the estimation of production of four calanoid copepods in Lindaaspollene, western Norway. – *Marine Ecology Progress Series* 45:57-68.
- Aksnes, D.L. & A.C.W. Utne 1997. A revised model of visual range in fish. – *Sarsia* 82:137-147.
- Bosch, H.F. & W. Rowland Taylor 1973. Diurnal vertical migrations of an estuary cladoceran, *Podon polyphemoides*, in the Chesapeake Bay. – *Marine Biology* 19:172-181.

- Bucklin, A., R. Sundt & G. Dahle 1996. The population genetics of *Calanus finmarchicus* in the North Atlantic. – *Ophelia* 44:29-45.
- Corkett, C.J., I.A. McLaren & J.M. Seigny 1986. The rearing of the marine calanoid *Calanus finmarchicus* (Gunnerus), *C. glacialis* Jaschnov and *C. hyperboreus* Kroyer with comment on the equiproportional rule. – *Syllogeus* 58. *National Museum of Canada* 58:539-546.
- Cronin, T.W. & R.B. Forward 1982. Tidally timed behavior: Effects on larval distribution in estuaries. – Pp. 505-520 in: Kennedy V. (ed.). *Estuarine Comparisons*. Academic press, New York.
- Eiane, K., D.L. Aksnes, & J. Giske 1997. The significance of optical properties in competition among visual and tactile planktivores: a theoretical study. – *Ecological Modelling* 98:123-136.
- Frasetto, R., R.H. Backus & E. Hays 1962. Sound-scattering layers and their relation to thermal structure in the strait of Gibraltar. – *Deep Sea Research* 9:69-72.
- Gade, H.G. & A. Edwards 1980. Deep water renewal in fjords. – Pp. 453-489 in: Freeland H.J., D.M. Farmer & C.D. Levings (eds). *Fjord Oceanography*. Plenum Press, New York.
- Hardy, A.C. 1936. Plankton ecology and the hypothesis of animal exclusion. – *Proceedings of the Limnological Society, Session 1935-6* 2:64-70.
- 1938. Change and choice: A study in pelagic ecology. – In: *Evolution: Essays on aspects of evolutionary biology*. Clarendon Press, London.
- Hardy, A.C. & E.R. Gunther 1935. The plankton of the South Georgia whaling grounds and adjacent waters, 1926-7. – *Discovery Reports* 11:1-456.
- Iles, T.D. & M. Sinclair 1982. Atlantic Herring: Stock discreteness and abundance. – *Science* 215:627-633
- Houston, A.I., J.M. McNamara & J.M.C. Hutchinson 1993. General results concerning the trade-off between gaining and avoiding predation. – *Philosophical Transactions of the Royal Society, London* 341:375-397.
- Kaartved, S. 1993. Drifting and resident plankton. – *Bulletin of Marine Science* 53:154-159.
- Kimmerer, W.J. & A.D. McKinnon 1987. Zooplankton in a marine bay. II. Vertical migration to maintain horizontal distributions. – *Marine Ecology Progress Series* 41:53-60.
- Lampert, W. 1989. The adaptive significance of diel vertical migration of zooplankton. – *Functional Ecology* 3:21-27.
- McLaren, I.A. 1963. Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. – *Journal of Fisheries Research Board Canada* 20:685-727.
- Ohman, M.D. 1990. The demographic benefits of diel vertical migration by zooplankton. – *Ecological Monographs* 60:257-281.
- Ohman, M.D., B.W. Frost & E.B. Cohen 1983. Reverse diel vertical migration: An escape from invertebrate predators. – *Science* 220:1404-1406.
- Sinclair, M. 1988. *Marine Populations*. – University of Washington Press, Seattle 252 pp.
- Skreslet, S. & N.Å. Rød 1986. Advection of *Calanus finmarchicus* between habitats in Norwegian coastal waters. – Pp. 375-387 in: Skreslet, S. (ed.). *The role of freshwater outflow in coastal marine ecosystems*. Springer-Verlag, Berlin.
- Stich, H.B. & W. Lampert 1981. Predator evasion as an explanation of diurnal vertical migration by zooplankton. – *Nature* 293:396-398.
- Wright, R. 1994. *The moral animal*. – Pantheon Books, Random House, New York. 466 pp.
- Wroblewski, J.S. 1982. Interactions of currents and vertical migration in maintaining *Calanus marshallae* in the Oregon upwelling zone - a simulation. – *Deep-Sea Research* 29:665-686.

Accepted 3 September 1997